Asexual and metasexual vertebrates

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John C. Avise, 2008. ***Clonality. The genetics, ecology, and evolution of sexual abstinence in vertebrate animals.*** New York, Oxford University Press: i-xi + 1-237. ISBN 978-0-19-536967-0

The focus recently attracted on "clones" by the sheep "Dolly" arose interest in the media for clonal reproduction, a phenomenon that had long been known by biologists. First discovered by the Swiss Charles Bonnet in 1740 in plant lice (Rostand, 1966), the reproduction of virgin females was called *parthenogenesis* by Owen (1849). In the 19th and 20th century, other unusual modes of reproduction were described under the terms of *gynogenesis*, *androgenesis*, *hybridogenesis*, etc. Most of these phenomena were first obtained artificially by embryologists in experimental conditions, often in amphibians, before being discovered in nature. Initially thought to be very rare and to occur mostly in "invertebrates", they were found to exist in several groups of vertebrates (fishes, amphibians and reptiles). This book proposes a review of some of these phenomena, called *clonality* by John C. Avise.

An original approach of this book is to consider clonality not only at the organismal, but also at the cellular (mitotic cell divisions) and molecular (DNA replication) levels: "*an individual can be viewed as a huge symbiotic colony of asexually derived clonemate cells*" (p. 13). This approach allows to realize that clonality is a very general feature of all living organisms and explains many of their properties.

At the organismal level, clonality is presented as the "*polar opposite*" of sexuality (p. 30). The evolutionary advantages of both systems are analysed and compared from a theoretical point of view. Nevertheless, the fact that both systems do exist in nature shows that none of them is completely superior to the other: according to the conditions, both systems can be efficient.

The book then proceeds to an overview of the characteristics of various unusual reproductive modes, starting with parthenogenesis, gynogenesis, "hybridogenesis" and related systems, then exploring other curiosities like polyembryony, hermaphroditic self-fertilization or human-sponsored clonality. All these strange phenomena are briefly described in a very clear language and pedagogic style. This lively text is not only descriptive but also offers many interesting reflections on the evolutionary meaning of the phenomena observed, often with original ideas, as can be expected from a brilliant theoretician of evolution as John C. Avise. Reading this book is both a pleasure and a very stimulating exercise, as it provokes thought and sometimes suggests views alternative to those of the author.

A real problem with this book, which is not particular to it but has long been a common feature of many "reviews" published by English-speaking authors (see e.g. in this respect the comments by Mayr, 1978), is its being largely "US-centered", as it displays a virtually complete ignorance of scientific literature in languages other than English. This is particularly annoying in a research field like descriptive and experimental embryology and related ones, where many of the publications, especially in the 19th and early 20th centuries, were published in German, French and sometimes other languages. The presentation both of the historical facts and of the theories in this book is therefore somewhat biased, although review papers and books on these questions exist in French and German. Nice biographical notes are provided about some United States researchers who significantly contributed to our knowledge of clonality in vertebrates, but the same is lacking for European workers. Hopefully, in a revised edition of this book, these lacks will be filled, perhaps through collaborations with European colleagues.

This book ignores a distinction that was introduced almost 20 years ago (DUBOIS, 1991) and that is important when dealing with such particular "reproductive modes". The latter formula is in fact misleading, as it mixes two very different phenomena: the mode of formation of the gametes (*gametogenesis*) and the mode of activation of the ovum to initiate the development of what then becomes the embryo (germinogenesis or better *kinetogenesis*, from the Greek *kineo*, "I move", to avoid a Latin-Greek "hybrid" term). Gametogenesis can be either sexual (with "normal" meiosis involving reductional divisions or *eumeiosis*), metasexual (with modified meiosis or *metameiosis*) or asexual (meiosis being absent and replaced by simple equational divisions or mitoses, i.e., *ameiosis*). Whereas phenomena like parthenogenesis, gynogenesis and androgenesis are modes of kinetogenesis, the "reproductive mode" often called "hybridogenesis" designates in fact a particular mode of gametogenesis. The embryonic development of the animals that show such a mode of gamete formation usually starts through a fully "normal" kinetogenesis, i.e., fertilization or *zygogenesis*. Mixing both phenomena obscures the analysis of these evolutionary situations, and suggests a misleading "parallelism" between parthenogenesis, gynogenesis and androgenesis on one side, and "hybridogenesis" on the other. As for the complex mechanisms recently described in salamanders of the genus *Ambystoma* under the general term of *kleptogenesis* (BOGART et al., 2007), it covers in fact two different phenomena, abnormal gametogenesis and mixed kinetogenesis processes, involving both zygogenesis and gynogenesis.

The term *hybridogenesis*, improperly stated in the book (p. 81) to mean "*the origin of hybrids*", has long been used in botany and zoology to designate the phenomenon of generation of an organism through hybridization between two organisms belonging in different species. A homonymous term was coined by SCHULTZ (1969) to designate the "reproductive mode" of some fishes, in which in fact it points to a particular kind of kinetogenesis. This term therefore entails several kinds of confusion and should be abandoned. In order to have more terminological clarity, DUBOIS (2008*a*) suggested to keep terms ending in *-genesis* form the categories of kinetogenesis, but to use differently formed terms, ending in *-poiesis*, for the categories of gametogenesis, five of which at least can be distinguished (DUBOIS, 2008*a*, 2009*b*). *Elasopoiesis* is the term that applies to the gametogenesis of so-called "hybridogenetic" organisms sensu SCHULTZ (1969), whereas *tychopoiesis* applies to the gametogenesis of so-called "kleptogenetic" organisms (BOGART et al., 2007). Elasopoiesis results in hemiclonal heredity, with one of the parental hemigenomes being transmitted complete and unmodified, or almost so, to all gametes, whereas tychopoiesis is a more complex mechanism resulting in meroclonal heredity, as it produces various kinds of gametes bearing one or several complete hemigenomes of variable origin, either maternal, paternal or both. Adoption of these distinctions would have made clearer some parts of the discussion of Avise's book.

For the same reason of inappropriate terminology, terms like *parthenogen* or *parthenogenetic* (as adjective or substantive), *gynogen* or *gynogenetic*, *androgen* or *androgenetic*, etc., should be avoided. Let us consider the term *hybridogen*. It is defined in the *Glossary* of Avise's book (p. 184) as "*An individual or strain that reproduces by hybridogenesis*". This definition is too broad and unclear. Individuals and strains are two different things. An individual organism can reproduce, but a strain cannot. We need different terms to designate organisms and strains, just like we have the terms *individuals* and *species* to designate organisms and the taxa in which they belong in the case of bisexual eumeiotic panmictic specions. The terms *hybridogen* or *hybridogenetic* are in fact particularly ambiguous as they may have *at least five* different meanings: (1) an individual *produced by* a phenomenon of hybridization, i.e., a first generation hybrid (this is the original and traditional meaning of the term, still of widespread use in botany), (2) an individual *produced by* a hybrid (second or subsequent generation), (3) an individual (of initial hybrid origin, but possibly many generations ago) *which produces* gametes by elasopoiesis, (4) an individual *produced by* gametes one of which at least resulted from an elasopoietic gametogenesis, (5) an individual which possesses *both* these latter particularities. In front of such a terminological confusion, it appears urgent to abandon completely this term, as well as the other ones ending in *-gen* mentioned above, and to use a clearly defined and non-ambiguous terminology. In the case of the term *androgen*, an additional confusion is due to its being identical to a well known term designating a male sex hormone.

In fact, the use of such terms in this book points to an uncertainty in the way such special organisms should be called. The book uses various formulae to designate them, including the terms discussed above but also "*parthenogenetic lineages*", "*unisexuals*", "*biotypes*", etc. It is not always clear what these terms actually mean, if they apply to individuals, taxa or other non-taxonomic units. Apparently, they just designate "kinds" of organisms, but do not refer them to formal *taxonomic units* or *taxa*. This point of view is difficult to support, because it would imply that only some of the organisms in the world belong to taxa, whereas some others are "outside taxonomy". In fact, this point is little tackled in the book, which does not present a clear position regarding the "species problem", except that in the *Glossary* (p. 189) the following definition is given for *species (biological)*: "*Groups of actually or potentially interbreeding individuals that are reproductively isolated from other such groups*". The taxonomic problems posed by the "special organisms" considered in the book are just mentioned in passing by Avise (e.g., p. 62), but not really discussed. Possibly this means that in his mind only bisexual organisms with normal gametogenesis and kinetogenesis, i.e. corresponding to the "Biological Species Concept" or BSC in the traditional sense (Mayr & Ashlock, 1991), can or should be treated taxonomically. But this would not be consistent with the basic requirement that, to be acceptable, taxonomic systems should be devised in such a way as to accommodate all organisms in the world, whatever their characteristics (Dubois, 1991: 70, 2005: 372). A quite different approach from that of Avise (and of most North American authors as well) has been proposed (Dubois & Günther, 1982; Dubois, 1991, 2007, 2008*a-b*, 2009*b*). This is based first on a clear distinction made between species as a *nomenclatural rank* and as a *taxonomic category*.

As a nomenclatural rank, the term *species* applies to a level in the nomenclatural hierarchy corresponding to the basic unit, the "brick", used in all disciplines of biological research (sometimes far away from evolutionary biology and systematics, like biochemistry, physiology, pathology, etc.), and also in all other non-scientific domains where organisms have to be unambiguously designated, such as environmental conservation, commerce, customs, laws, etc. This is the most widespread use of the term species. In this context, all organisms alive must be uniformly referable to a taxonomic unit of species level, designated by a Latin binomen, that may appear in faunistic lists, juridical texts, etc. For this purpose, it is not appropriate to designate some taxa ("biological species") by Latin binominals, and others by letters or combinations of letters (such as *Poeciliopsis* Cx or *Ambystoma* LLJA) or compound names (such as *Poeciliopsis monacha-lucida*).

As a taxonomic category, the term *species* may designate various kinds of units, according to the biological properties of the organisms at stake. In order to distinguish this acceptation from the nomenclatural one, these units may be known under the general term of *specion* (Dubois, 2007, 2008*b*), and the different kinds of specions may be designated by terms ending in *-on*, like taxon. The "common" situation is that of the "biological species" or *mayron* (Dubois, 2007), a bisexual panmictic unit whose gene pool is protected from those of other similar units by ecological, ethological, mechanic, biochemical, chromosomal, genetic or other barriers. But other kinds of units can be recognized. These include taxa that depend for their reproduction on other taxa which they so to speak "parasitize" sexually at each generation, either through gynogenesis or through genuine fertilization, and for which the term *klepton* was coined (Dubois & Günther, 1982), as well as unisexual female taxa that reproduce through apomictic or automictic parthenogenesis, which can be known under the term of *klonon* (Dubois, 1991). Several other subcategories can be recognized, and probably some have not yet been identified so far in nature. The general term *kyon* has been proposed for all these categories of "strange species" reproducing through clonality (Dubois, 2008*a*, 2009*b*).

In Europe, most authors use the category klepton (derived from the Greek term *kleptos*, "thief", not from the term *kleptomania*, as wrongly stated by Avise, p. 99) for ranid green frogs of the genus *Pelophylax*, but this has not been adopted by most North American authors. The reluctance of the latter to use special taxonomic units for these entities implies in some cases that they do not want to recognize them as taxa. For example, Frost & Hillis (1990) argued that these frogs with special gametogenesis should be referred formally to the species with which they breed at each generation, just like males are members of the same species as the females with which they breed! This mode of reasoning by analogy is wrong, as in bisexual species males and females are inter-dependent, which is not the case in systems like that of European green frogs, where the klepton indeed depends from the associated mayron for its reproduction, whereas the reverse is not true (see Dubois, 2008*a*: 2009*b*). Others apparently think that these special organisms belong in distinct evolutionary units, which they call "biotypes" or "unisexuals", but must be kept "outside taxonomy" as they are not "biological species" But the a priori idea that all organisms on earth should belong in a single taxonomic category, a "*unified concept of species*" (e g , DE QUEIROZ, 1998), has no theoretical or empirical justification, and only seems to stem from a reductionist scientific attitude. For any evolutionary biologist accustomed to the diversity and unpredictability of life, it is no surprise to realize that different kinds of basic evolutionary units do exist in nature, that cannot be unified except artificially Be it as it may, it is clear that a discussion of the taxonomy of clonal, hemiclonal or meroclonal organisms with asexual or metasexual gametogeneses is wanting in Avise's book, as well as a discussion of the different nomenclatural systems proposed for these taxa (see DUBOIS & GUNTHER, 1982, DUBOIS, 1991, 2008*a*, 2009*b*) Hopefully this will appear in a subsequent edition of this exciting book

This book contains many other interesting discussions, some of which occupy only a few lines but stimulate interesting thoughts. They cannot all be surveyed here, but let us just take one example, which opens a reflection on the conflict that exists nowadays between evolutionary biology and taxonomy on one side, as disciplines which aim at a better understanding of biodiversity on this planet, and conservation biology on the other, which sometimes acts as a break against this progress of knowledge (DUBOIS, 2003, 2006*b*, 2009*a*,*c*; DUBOIS & NEMÉSIO, 2007; NEMÉSIO, 2009): "*( ) the traditional kinds of data initially suggestive of unisexuality ( ) seem to be gathered less often now because museum workers and systematists generally tend to collect fewer vertebrate specimens. This restraint is due to ethical concerns about declining biodiversity, as well as to stricter laws and protective regulations for vertebrate animals*" (p. 51).

Pursing reflection on these questions leads to realize that, in order to be able to protect some of the extraordinary organisms of multispecific origins that occur in some of these systems, like in the genus *Ambystoma* (BOGART et al , 2007, BI et al , 2009), we need to recognize formally special taxa for them, and to provide them with Latin nomina, as this is indispensable for placing them on official lists of protected taxa (DUBOIS, 2006*a*)

A last comment of general value here concerns these multihybrid organisms. Their mitochondrial genome may in some cases originate from a mayron the nuclear genome of which is totally absent in their genotype (BOGART et al , 2009), so that identifying them through "barcode" would result in a completely wrong taxonomic allocation This suggests that great care should be taken in the use of barcode, as long as so little is known about the gametogenesis and kinetogenesis of most living organisms.

Well, these "strange species" still have a lot to tell us and they no doubt reserve a lot of surprises to biology Rigid-minded people will perhaps be disturbed by these findings, but it is certainly more exciting to learn from nature than only from our models and theories...

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